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REPRODUCTION, POPULATION CHANGES AND INTERACTIONS OF SMALL MAMMALS ON A NATURAL AREA IN NORTHEASTERN KANSAS

by

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INTRODUCTION

Ecological succession in a plant community and its associated small mammals is here traced over a 32-year period in a 2 ha study plot (Figs. 1 and 2) on the University of Kansas Natural History Reservation in Douglas County. Formal sampling with an established grid of live-traps was maintained from March 1950 through January 1955 and from March 1979 through June 1981. In each of the intervening years some live-trapping was carried on. Sampling of plant and animal life was most intensive and continuous just before the removal of livestock in 1948 and in the subsequent years through 1954. In 1964 and 1980 vegetation of the plot was reanalyzed. The grid of mammal live-traps was reactivated late in 1978 with intensive sampling through 1979, 1980 and early 1981 (Table 1). Successional change in the plant and animal life was found to be exceedingly rapid in the early years after protection was initiated and the vegetation was released from grazing by livestock, but became progressively more gradual in later years.

The 13 species of small mammals captured on the study plot are fairly well known ecologically, and some have been the subjects of detailed field studies in this same general area. However, our data provide new insights into their roles in succession, their habitat selection, and the ecological interactions among them.

Three grassland species, the Prairie Vole, Hispid Cotton Rat and Western Harvest Mouse, all underwent parallel population change, increasing from virtually zero to spectacularly high population density within the course of a few generations. Then they decreased but with

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constant minor fluctuations which must have affected many of their community associates. Each of the other species also affected the community, somewhat in proportion to its size and abundance.

METHODS AND MATERIALS

Study plot. The area, ''House Field'', near the center of the northwest quarter of the northeasternmost section (4) of Douglas County, township 12S, range 20E, is sloping, 280 to 290 meters elevation, at the base of a south-facing hillside, 320 m long and from 152 m wide at its western end to 43 m wide near its eastern end (Figs. 1 and 2). In 1948 it was an open meadow dominated by the introduced pasture grass, Smooth Brome, and had about two dozen scattered large trees, mostly American Elm but with one or more each of Black Walnut, Honey Locust, Osage Orange, and Kentucky Coffee Tree. For many years the area had been heavily grazed by livestock. By late summer of each year little herbaceous vegetation remained. Presumably the area originally had been bluestem prairie, and a few well scattered clumps of Big Bluestem were still present in 1981.

TABLE 1. Summary of Small Mammal Trapping on ''House Field'' Grid, University of Kansas Natural History Reservation.

	Date							
Species	1950	1951	1952	1953	1954	1979	1980	TOTAL
Prairie Vole								
individuals captured	587	541	448	233	107	16	5	1937
total captures	3232	3374	2614	1014	451	30	7	10722
White-footed Mouse								
individuals captured	50	127	102	49	26	53	38	445
total captures	191	443	406	129	76	106	82	1433
Deer Mouse								
individuals captured	28	36	17	25	10	0	0	116
total captures	159	148	86	72	34	0	0	499
Pine Vole								
individuals captured	23	64	8	18	7	1	1	122
total captures	63	766	59	76	25	4	1	994
Western Harvest Mouse								
individuals captured	109	163	114	86	9	4	2	487
total captures	527	523	455	326	16	6	2	1855
Hispid Cotton Rat								
individuals captured	5	86	27	0	0	1	0	119
total captures	53	454	172	0	0	4	0	683
All species combined								
individuals captured								3226
total captures								16186
Days of trapping	84	74	98	80	39	53	25	453

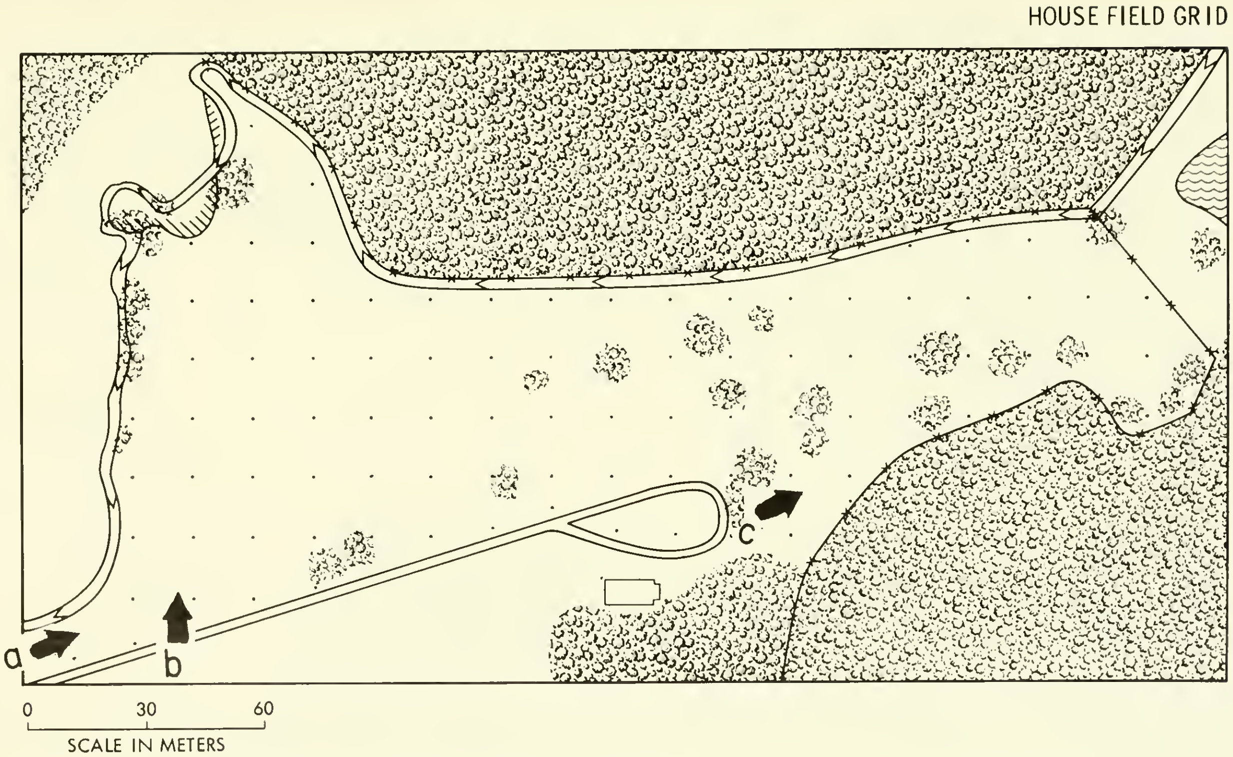

FIGURE 1. Map of study plot with live-trap grid in House Field, University of Kansas Natural History Reservation, showing main types of vegetation and their distribution in 1950, 2 years after livestock were excluded; unshaded is grassland.

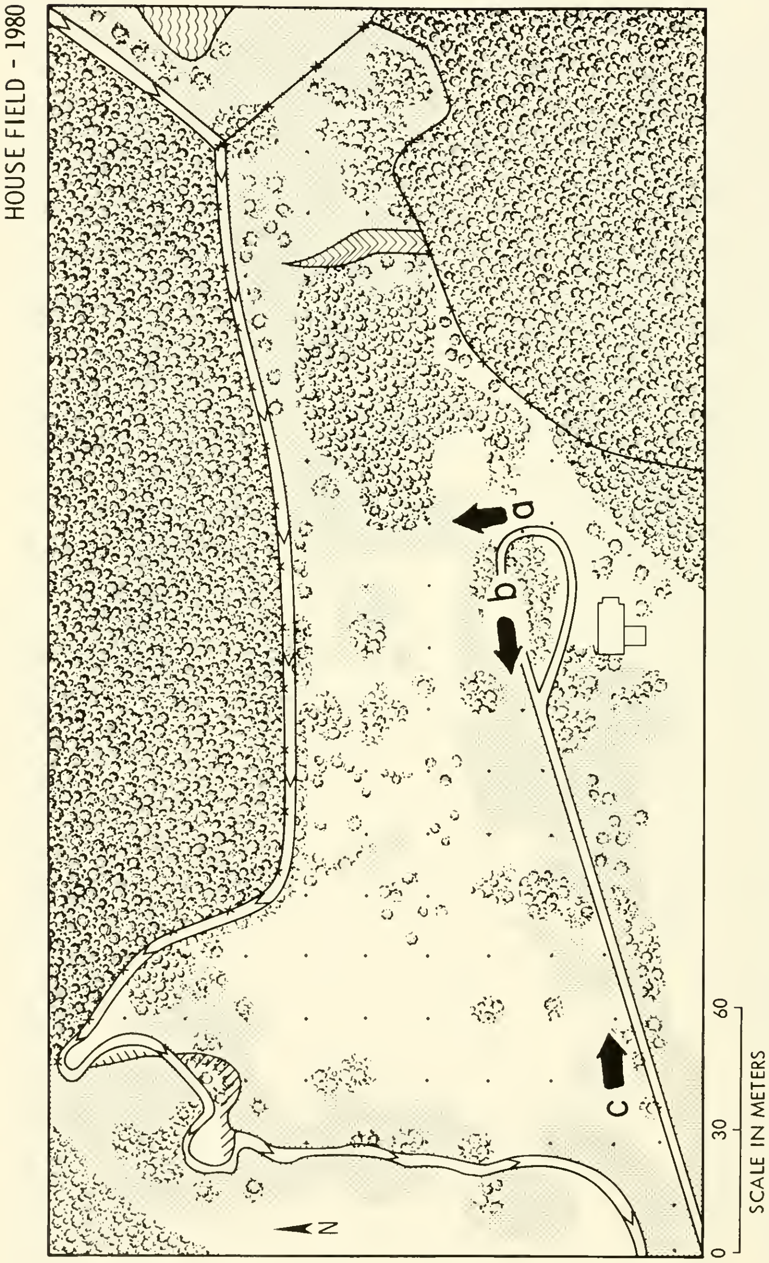

FIGURE 2. Map of study plot as in Fig. 1, in 1980 when trees and shrubs (stippling) had spread into formerly open areas.

Lasting effects of different treatments during this study and earlier were noticeable. An area of perhaps 1000 m^2 northwest of the headquarters building, that had been stripped of sod in the early 1940s, had a scanty vegetation, with Common Lespedeza and Threeawn Grass indicative of depauperate soil. A similar sized area northeast of the headquarters, which had been a sheep corral in the early 1900s, was dominated in the early 1950s by Giant Ragweed and other coarse weeds, and later by a dense thicket of Wild Plum, with other tall shrubs and saplings. The first area had the greatest concentration of records for the Deer Mouse and the second had the greatest concentration of cotton rats in 1950–53.

During the interval between the trap samplings of 1950–1953 and 1978–1980, a small part of the area to the south and northeast of the headquarters building was cleared of brush, the dense stand of tree saplings was thinned and the low vegetation was maintained as a lawn. That portion south of the building, a small percentage of the total, was excluded from the trap grid in the 1978–1980 sampling.

Vegetation sampling. General notes concerning the vegetation were recorded from time to time beginning before the trap grid was established in 1948. In later samplings on series of 3.55 m^2 plots, plants were classified according to species, composition, height and density. Further information was obtained by study of aerial photographs and by mapping the dominant vegetation within each square of the trap grid.

Mammal sampling. Mammal sampling was first attempted in August 1948 while livestock were still on the area, with a line of 50 snap traps baited with rolled oats and peanut butter, but in several hundred trap nights no catches were made. This first trap line was approximately 200 m southwest of the subsequently established grid, in the same field.

The grid of live-traps was first established in March 1950. The model used was the "Fitch-trap" made of hardware cloth with a pendulous trigger mechanism, with an attached can for a nest box, containing insulating material and a supply of food (Fitch, 1950; Rose, 1973). Traps varied slightly in details of the trigger mechanism, and in size and shape of the nest box. There were 100 traps in the grid, with 19 north-south rows and a spacing of approximately 15 m (50 feet) between traps.

Trapping procedures varied somewhat according to season and weather conditions; the traps were usually kept set for approximately a week out of every month, in a run of consecutive days. However, lengths of trapping periods varied and operations were sometimes curtailed because of extremes of weather or disturbance of the trap-line by predators. Each mammal live-trapped was individually marked by toe-clipping (combined with ear-clipping in some; Fitch, 1952). At each capture, the animal's identifying formula, sex, breeding condition, weight, and capture site, along with any other information considered noteworthy (parasite infestations, injuries or abnormalities), were recorded (see Tables 2 and 3). Each animal was processed at its capture site and released, following only a few seconds of handling.

Perforate vaginas in oestrus and conspicuously distended abdomens in late pregnancy constituted signs of reproductive activity that were rou-

TABLE 2. Comparative Statistics for Four Rodent Species on House Field Trapping Area, Based on 100 Randomly Selected Individuals of Each.

	Species			
Statistic	Prairie Vole	Western Harvest Mouse	Hispid Cotton Rat	Deer Mouse
Mean number of captures per animal	3.1	3.5	5.2	5.2
Maximum captures per animal	12	19	45	24
Mean span of records (days)	31.3	39.0	31.4	48.5
Maximum span of records (days)	217	274	287	436
Mean shift between successive captures (meters)	26.91 (9.91)*	41.83 (24.88)*	30.73 (16.08)*	40.48 (24.89)*
Maximum shift between successive captures (meters)	130	168	183	198

*Including "no movement" records in average.

tinely recorded and were the bases for gauging the level of reproduction, as indicated in Tables 4 and 5. For Prairie Voles, in 1950 and 1951 relatively large monthly samples were obtained, but for these voles in other years and for the remaining species in each year of the study, samples were smaller. Those samples that contained few animals were of limited significance separately but were useful collectively to show trends.

Although 24 years intervened, from 1955 through 1978, when the trap grid of the study plot did not function, various types of observations kept us informed regarding the status of the small mammal population. The first and second authors were resident on the area throughout the interval. A grid of mammal traps comparable to that of the study plot was established on a hilltop old-field 380 m northeast, and was in operation over the ten-year period, 1954 through 1963, accumulating approximately 7000 records. Wire funnel traps for snakes, with drift fence installations, were operated on many parts of the Reservation, including the study plot, over the years, 1957–1963 and 1977–1981. These traps often caught small mammals also, including shrews and jumping mice not readily attracted to bait, and poorly represented in the samples from the mammal traps.

During the periods of sampling with the trap grid, three sorts of figures were obtained to show numbers of small mammals (Table 6). For the Prairie Vole, which was represented by relatively large samples, capture-recapture ratios were used and were refined by the so-called Jolly Method

TABLE 3. Comparison of Vagility in Four Species of Small Mammals on Study Plot, as Reflected by Mean Distance (Meters) between Successive Capture Sites.

	Excluding "no movement" recaptures		Including "no movement" recaptures	
	♂	♀	♂	♀
Prairie Vole	26.2 ± 3.77 in 22	28.1 ± 1.15 in 53	8.7 ± 1.98 in 66	11.0 ± 1.04 in 134
Hispid Cotton Rat	34.3 ± 2.32 in 186	28.5 ± 1.88 in 90	20.2 ± 1.65 in 314	13.3 ± 1.81 in 192
Western Harvest Mouse	85.4 ± 2.96 in 101	44.2 ± 4.32 in 65	32.3 ± 2.34 in 167	29.3 ± 3.41 in 98
Deer Mouse	46.2 ± 5.38 in 138	28.6 ± 2.12 in 102	32.8 ± 2.47 in 194	16.9 ± 1.68 in 172

TABLE 4. Percentages of Adult Females Breeding in Pooled Monthly Samples, 1950–1954.*

	Mean Temp. (°C)	Mean Precip. (mm)	Prairie Vole	Hispid Cotton Rat	Deer Mouse	White-footed Mouse	Western Harvest Mouse	Pine Vole
Jan.	−1.17	27.7	36.1(300)	0(35)	23.0(13)	0(15)	4.2(48)	44.1(34)
Feb.	0.4	34.0	50.1(251)	0(20)	23.3(30)	30.0(10)	8.8(34)	36.1(42)
Mar.	6.89	55.0	57.6(302)	0(23)	31.0(58)	50.0(44)	49.6(123)	45.7(106)
Apr.	12.83	79.7	63.0(338)	70.0(10)	17.6(34)	46.2(26)	69.0(74)	39.6(154)
May	18.17	124.0	60.9(579)	83.2(6)	27.3(33)	36.4(11)	44.7(85)	40.7(135)
June	23.28	118.8	44.7(670)	28.6(14)	25.0(16)	48.3(29)	44.8(29)	30.8(65)
July	26.17	95.2	43.0(535)	27.2(11)	25.0(8)	35.7(28)	33.9(62)	14.3(14)
Aug.	25.28	94.0	43.6(606)	70.4(27)	61.5(26)	75.6(41)	61.4(44)	47.0(17)
Sept.	21.0	113.0	51.9(540)	78.6(14)	37.6(8)	63.5(11)	45.0(20)	66.6(18)
Oct.	14.0	72.6	50.5(594)	29.1(55)	25.0(24)	22.7(22)	13.3(17)	60.0(15)
Nov.	7.06	55.9	34.2(340)	7.9(127)	39.0(36)	3.4(58)	35.7(28)	7.1(14)
Dec.	0.56	29.7	29.8(198)	0(36)	5.3(19)	2.9(35)	11.0(18)	0(6)

*Figures in parentheses show number of adult females in each sample.

TABLE 5. Percentages of Adult Female *Microtus ochrogaster* Visibly Pregnant in Monthly Samples, 1950–1955.

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1950	--	--	5.8	8.0	21.0	13.3	57.3	43.8	40.4	45.2	7.0	0
1951	2.3	0	0	19.4	37.1	14.9	6.7	15.2	15.0	21.9	8.9	0
1952	0	10.4	22.6	22.6	29.5	16.5	7.9	10.8	20.3	18.9	3.3	0
1953	0	9.1	13.3	27.5	39.4	5.5	3.8	12.5	6.2	10.0	23.0	8.3
1954	4.8	3.6	9.1	33.3	--	--	--	--	--	36.6	63.4	10.0
1955	7.1	--	--	--	--	--	--	--	--	--	--	--

(Krebs, 1972). These figures are probably the most accurate. For other species the number of recaptures from one sampling period to another was usually small, and for these, simple capture-recapture ratios (Petersen Index) were used. When samples included no recaptured animals from the previous sampling period, preventing use of a capture-recapture ratio, the numbers actually captured were assumed to represent the population present.

Small mammal community and associates. The six species of small mammals captured in the trap grid with sufficient regularity to yield demographic data were the Prairie Vole, White-footed Mouse, Deer Mouse, Western Harvest Mouse, Hispid Cotton Rat and Pine Vole. Each of these had a much different history on the area during the course of the study, and we have undertaken to explain the changes in each in terms of its habitat selection, reproduction, spatial relationships and changes in the area itself.

Additional species of small mammals were recorded on the area, but were not numerous enough there to yield demographic data. These were the following:

Eastern Wood Rat: One adult male was captured in 1980 on the western edge of the plot beside a gully cutbank. It was a wanderer from optimum habitat of the hilltop limestone outcrops where most are found and its appearance on the plot was coincident with a strong recovery on the general area after a drastic reduction in 1949–50 and several succeeding years (Fitch and Raney, 1956).

Great Plains Harvest Mouse: Several were trapped on the plot in 1950, but at first they were not recognized as distinct from the much commoner Western Harvest Mouse, and they soon disappeared from the plot as succession eliminated their shortgrass habitat.

House Mouse: This introduced species was captured in small but variable numbers, with some records in each year of trapping.

Meadow Jumping Mouse: This mouse was caught in the trap grid only occasionally because of its indifference to the grain bait used. However, the combined record of captures in the mammal trap grid and in wire funnel traps up into 1980, indicated that it was present in low numbers throughout the entire period of our study.

TABLE 6. Estimated Numbers of Each Common Rodent Species of Study Plot, 1950–1954, as Indicated by Capture-Recapture by Jolly Method (Prairie Vole) or Actual Capture*; Figures in Parentheses Represent Latter Part of the Month.

	Species					
Date	Prairie Vole	Pine Vole	Hispid Cotton Rat	White-footed Mouse	Deer Mouse	Western Harvest Mouse
1950						
March	70(90)	20	–	7	27	90
April	103(106)	13	1	29	18	45
May	143(208)	16	4	24	30	134
June	223	2	6	38	13	122
July	188(200)	–	7	15	24	95
August	188(205)	–	4	16	12	80
September	167(147)	6	1	20	10	46
October	179(196)	18	3	30	14	94
November	198(188)	9	2	26	16	54
December	189	6	1	55	23	115
1951						
January	188	10	–	38	26	118
February	216(221)	33	–	43	10	124
March	258	48	–	33	5	98
April	265(199)	51	1	80	13	66
May	334	41	22	44	20	49
June	394	27	99	61	16	38
July	282(268)	28	32	32	12	60
August	221(211)	20	60	46	3	38
September	185	24	80	14	2*	4*
October	165	30	65	59	–	81
November	192	23	54	39	4	135
December	269	24	37	29	3	83
1952						
January	191(191)	28	25	36	6	74
February	199(194)	38	15	24	8	89
March	196(176)	34	24	39	18	80
April	128(98)	37	16	21	11	52
May	123(116)	32	8	4	5*	47
June	74	12	3	16	7	52
July	54	2	–	30	4	144
August	47	–	–	28	2	44
September	62	–	–	22	2*	48
October	48	8	–	33	–	32
November	48	4	–	9*	–	30
December	38	–	–	15*	1*	50
1953						
January	91	–	–	13*	3*	18
February	130	–	–	18*	5*	40
March	98	20	–	14*	13*	59
April	196	22	–	13*	10*	36
May	205	10	–	2*	1*	22
June	133	–	–	3*	–	28
July	103	–	–	4*	–	70
August	80	1	–	4*	–	20
September	192	7	–	8*	–	8*
October	79	1	–	1*	–	4

Table 6. Estimated Numbers of Each Common Rodent Species of Study Plot. (Concluded)

	Species					
Date	Prairie Vole	Pine Vole	Hispid Cotton Rat	White-footed Mouse	Deer Mouse	Western Harvest Mouse
November	68	–	–	2*	–	5
December	68	–	–	6*	1*	3*
1954						
January	78	–	–	10*	3*	5
February	56	–	–	3*	4*	6*
March	13	–	–	2*	1*	5*
April	55	–	–	4*	2*	–
May June July August September	————trapline not in operation————					
October	138	–	–	9*	1*	–
November	18	2	–	8*	2*	–
December	10	3	–	–	–	–

Least Shrew: This shrew was always poorly represented in samples because of low numbers, but also because it was not attracted by grain bait, and was too small and light to trip the trap triggers consistently. Several were caught in funnel traps, 1979–81, indicating that it had not undergone drastic reduction despite successional changes.

Short-tailed Shrew: This shrew was caught in small numbers throughout the period of our study, with no important population changes detectable.

Southern Bog Lemming: The lemming was not present on the study plot, 1948–54, but became prominent in the 1960s. A single adult male was caught in the 1979–80 sampling.

Fox Squirrels, Gray Squirrels, Eastern Cottontails and Eastern Moles also lived on the study plot, but because of size or habits, were not sampled in the grid of live-traps and hence are not included in this report. Neither were larger mammals, including the Woodchuck, Opossum, Striped Skunk, Spotted Skunk, Long-tailed Weasel, Gray Fox, Red Fox, Raccoon, Coyote, and White-tailed Deer, which were seen on the area from time to time. Besides the native carnivores in the list above, domestic and feral cats, one species of hawk, three species of owls and eight species of snakes were important predators on the small mammals of the plot.

RESULTS

Plant succession. When our observations began in 1948, the area had been subjected to disturbance for more than 80 years and its original vegetation, presumably that of a bluestem prairie, had been much altered. The grasses, Smooth Brome and Kentucky Bluegrass, various seral weeds, and the tree, Osage Orange, all introduced, were commoner and more conspicuous than most native species.

The first sampling was made in September 1948, when the area was still subject to heavy grazing by horses and cattle. Droppings of these animals occupied an appreciable percentage of the ground surface. Extensive areas were trampled and almost bare, but in other sites ground vegetation was from 2.5 to 30 cm high. Along with the dominant grasses, Smooth Brome and Kentucky Bluegrass, weedy forbs of types relatively unpalatable to livestock, including spurges, nightshades and composites, were conspicuous. A year later, near the end of the first growing season free from grazing, the crop of vegetation was abundant and varied with coarse weeds making up a major part of it (Plate I, a). The dominant tall weed was Ironweed with also Hoary Vervain, Tall Thistle, Philadelphia Fleabane, Common Sunflower, Pokeweed, and Wild Lettuce standing out above the grass, and with lower weeds, including Buffalo-bur, Carolina Nightshade, Ground Cherry, Flowering Spurge, mixed with grass layer. Smooth Brome was the dominant grass and Kentucky Bluegrass, second; others included Muhly Dropseed, Witchgrass, Stinkgrass, Green Foxtail, Barnyard Grass, Crabgrass, Japanese Chess, and Purpletop.

In the late summer of 1951 (see Fig. 1) all the same species were still present, but different parts of the field were dominated by Smooth Brome, Ironweed, Wild Lettuce, American Germander, and Common Lespedeza, respectively. Coralberry, already beginning to invade, was a forerunner of the woody species that would eventually replace many of the herbs. In 1951 (Plate I, b and c) the crop of vegetation was both luxuriant and highly varied. Sedge was prominent as a result of unusually heavy precipitation. Two Blackberry patches, each several meters in diameter, had developed. Numerous tree seedlings were in evidence, especially American Elm, Honey Locust and Osage Orange. Vines, including Fox Grape, Greenbrier and Virginia Creeper, had grown up in shaded sites. Weedy plants, including Buffalo-bur, Carolina Nightshade, Cheese Mallow, Common Ragweed, Curly Dock, Flowering Spurge, Goatweed, Ground Cherry, Hoary Vervain, Ironweed and Woolly Croton, were less common than they had been in the preceding two years. Grasses, mainly Smooth Brome and Kentucky Bluegrass, were replacing the weedy forbs; Crabgrass, Purpletop and Witch Grass were also present.

By 1980 the area had changed strikingly. Forest had closed in on its eastern one-third, with an almost continuous leaf canopy developed by the many young trees (Fig. 2 and Plate II). Heights of 9 m and DBH of 20 cm were common in these trees. The western two-thirds of the area had developed into a mosaic of open patches retaining herbaceous vegetation, alternating with brush patches and trees or tree clumps. The shrub patches were Rough-leafed Dogwood, Smooth Sumac, Blackberry and Wild Plum, in that order of importance. In the more open western part approximately 50% of the trees were Osage Orange, with the remainder almost evenly divided between walnut, Honey Locust, American Elm and Red Cedar. In the eastern part cedar was absent and Osage Orange was less abundant; the order of abundance was approximately: Black Walnut,

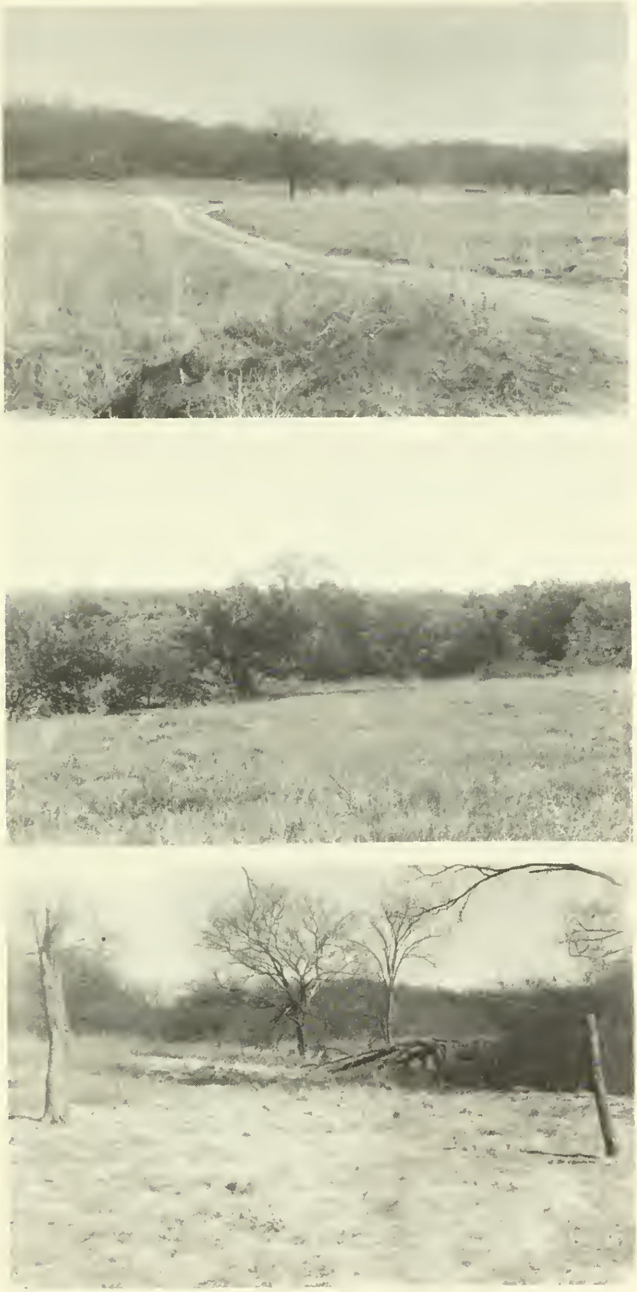

PLATE I. Three views of the study plot from 1949 to 1951 showing open terrain with absence of brush and young trees. Views "a" (upper, December 1949), "b" (middle, August 1951), and "c" (lower, December 1951) correspond to arrows in Figure 1, and show position and direction of camera.

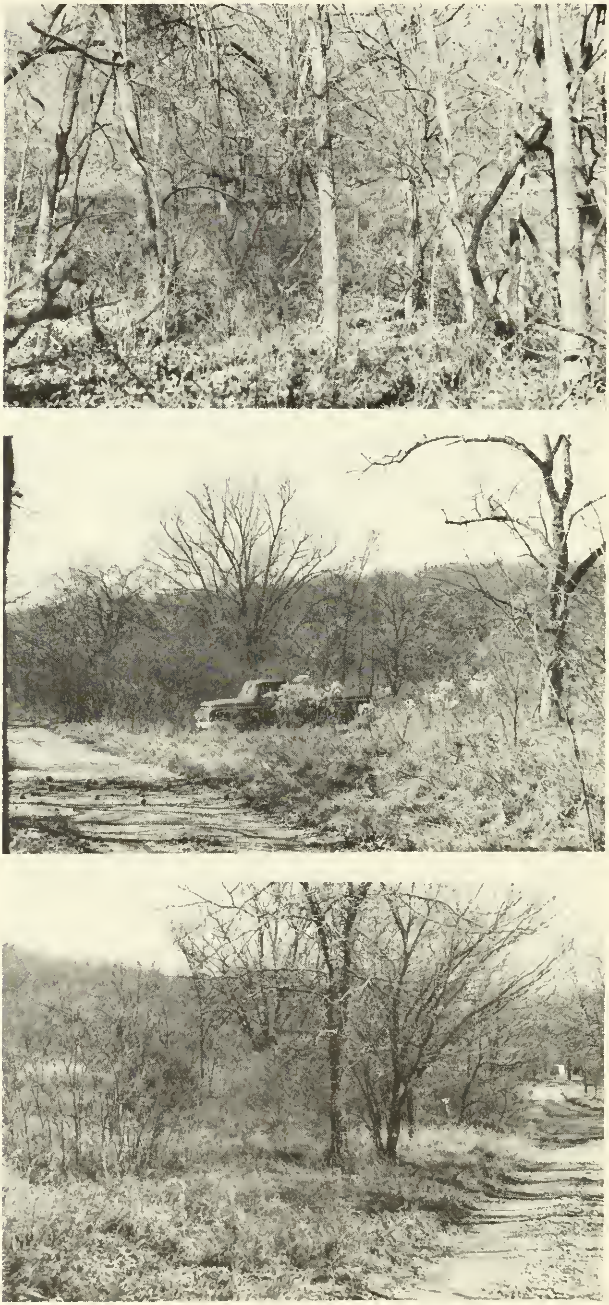

PLATE II. Three views of study plots in November 1981 showing invasions by trees and shrubs. Views "a" (upper), "b" (middle), and "c" (lower) correspond to arrows in Figure 2, and show position and direction of camera.

Hackberry, Osage Orange, Honey Locust, Mulberry and American Elm. Smooth Brome continued to dominate most. Vegetation was still affected on the area stripped of sod in the 1940s. Broomsedge, Aster, Missouri Goldenrod and Sumpweed were prominent there but not elsewhere. Weedy plants formerly abundant on the area which had disappeared completely or dwindled to negligible amounts included: Ironweed, Tall Thistle, American Germander, Ground Cherry, Buffalo-bur, Hoary Vervain, Snow-on-the-mountain and Woolly Croton.

Numbers and biomass. The populations of small mammals on the study plot changed rapidly, with constant fluctuations in total numbers and in composition according to species. Trends during the annual cycle and longtime trends were, to some extent, obscured by the rapid changes and reversals that sometimes took place from month to month. Such changes seemed to be controlled largely by vagaries of the weather. Predation was doubtless important also. Our maintenance of the grid of live-traps must have influenced the population in various ways—by occasional mortality in traps and perhaps more serious mortality in recent litters when females were detained in the traps, and by providing a supplementary food supply of grain bait. Such influences are difficult to evaluate.

Plant succession on the area and its effect on small mammal populations may be summarized as follows. 1948: The hardy exotic grasses, Smooth Brome and Kentucky Bluegrass, had largely replaced native prairie grasses but were kept cropped close by livestock. Unpalatable coarse weeds including various spurges, composites and nightshades were prominent. For small mammals the habitat was deficient in food and especially in shelter. The Deer Mouse was probably the only species present on the area, but the White-footed Mouse was common along the edges in adjacent woodland. 1950: With release from grazing pressure, the area had produced an abundant and diverse crop of herbaceous vegetation. Many different species, including Smooth Brome and Kentucky Bluegrass, dominated different parts of the area. Ground litter had begun to develop on some more mesic parts of the area providing sufficient cover for vole runways, but in some places there were still patches of bare ground. Abundant food and cover were available for small mammals. The Western Harvest Mouse appeared and increased to a high population with remarkable rapidity over a few months. The Prairie Vole responded almost as promptly and reached even higher densities. Eleven other species also appeared and increased during the course of the year. 1951: Excessive precipitation in the spring and summer resulted in an even more luxuriant crop of grass-weed vegetation than that of 1950. Seedlings of bushes and trees were abundant, but still were only a small part of the crop of vegetation. Ground litter accumulated. Small mammals continued to increase during the early months of 1951, but then in a sudden reversal of the trend, underwent drastic reduction. The reduction coincided with increase in the cotton rat population, and predation by the rats was believed to have been a major cause of mortality in other species. 1955: This was the fourth relatively dry year after the unusually heavy precipitation of 1951. Each year brought about further progressive change in the herbaceous vegetation, with grass, especially Smooth Brome, gaining dominance, and various weedy forbs dwindling. At the same time woody plants, Dogwood, Coralberry, Crab Apple, Wild Plum, and young trees of many species, were encroaching, mainly along the edges, and beginning to crowd out the herbaceous growth. The many kinds of plant food formerly available in the diversified flora of early succession at different seasons and with different plant parts, had mostly become scarce or had disappeared. Small mammal populations of all species present had undergone drastic decline, ostensibly because of the reduced food supply. 1980–1981: Trees and shrubs had continued to encroach on the area, and covered about half of it in a mosaic pattern. Smooth Brome dominated the spaces between trees and brush clumps, with little weedy vegetation remaining. The White-footed Mouse as a woodland and woodland edge species, was by far the most numerous small mammal present, but its numbers were well below 1950–1953 levels. The other species present in the early years of sampling still persisted (with one exception) but only as stragglers of a few individuals each, limited to scattered points on the plot.

For each small mammal species, the stage of plant succession when a population peak was attained, the type of habitat then occupied, and the microhabitat of its final refugium on the plot are significant items for an understanding of its autecology. The Deer Mouse, requiring open areas and patches of bare ground, was first to reach its population peak early in the second growing season (1950), after removal of livestock, and was first to disappear. The Prairie Vole, Pine Vole, Hispid Cotton Rat and White-footed Mouse all reached their peak populations, April to June 1951, when herbaceous vegetation had reached its maximum biomass and diversity. The Western Harvest Mouse reached maximum numbers in June 1952 when the grass crop was at its maximum, as grass seeds are the mainstay of its diet. By late 1954, after three successive summers that were drier than usual with grass replacing forbs and woody plants replacing herbs, Prairie Voles had declined to levels far below the maximum, and the five other dominant species had either disappeared from the plot or dwindled to a few individuals there. During the following 25 years succession was relatively gradual, and changes in the numbers of small mammals was relatively small, including slight temporary gains when weather and other combinations of factors permitted them, followed by corresponding reductions.

It might have been expected that a high incidence of reproductive activity would have been followed routinely by an increase in the population that would show up in sampling after a lag of a few weeks, allowing time for the gestation, birth, and weaning of new animals. Actually, no such correlation was noted in most instances, and it seemed that increased reproduction was followed by an exceedingly high mortality of young in the nest. Predation was probably the main cause of mortality in young in the nest, and must have been to a large extent density dependent.

Table 6 shows the changing levels over a five-year period. The Prairie Vole was almost always the most numerous species and usually outnumbered all other species combined. Table 7 shows the estimated biomass of the population by months for each of four years, 1950 through 1953. It shows that biomass increased through 1950 to a peak in mid-1951 then gradually decreased to a low level in late 1952. After small gains in the early springs of 1953 and 1954, it decreased again in each of these years during drought summers (see Fig. 3 and Table 7). In 1979 biomass was much below the levels of 1950–54.

Biomass calculations (Fig. 3 and Table 7) were based upon the

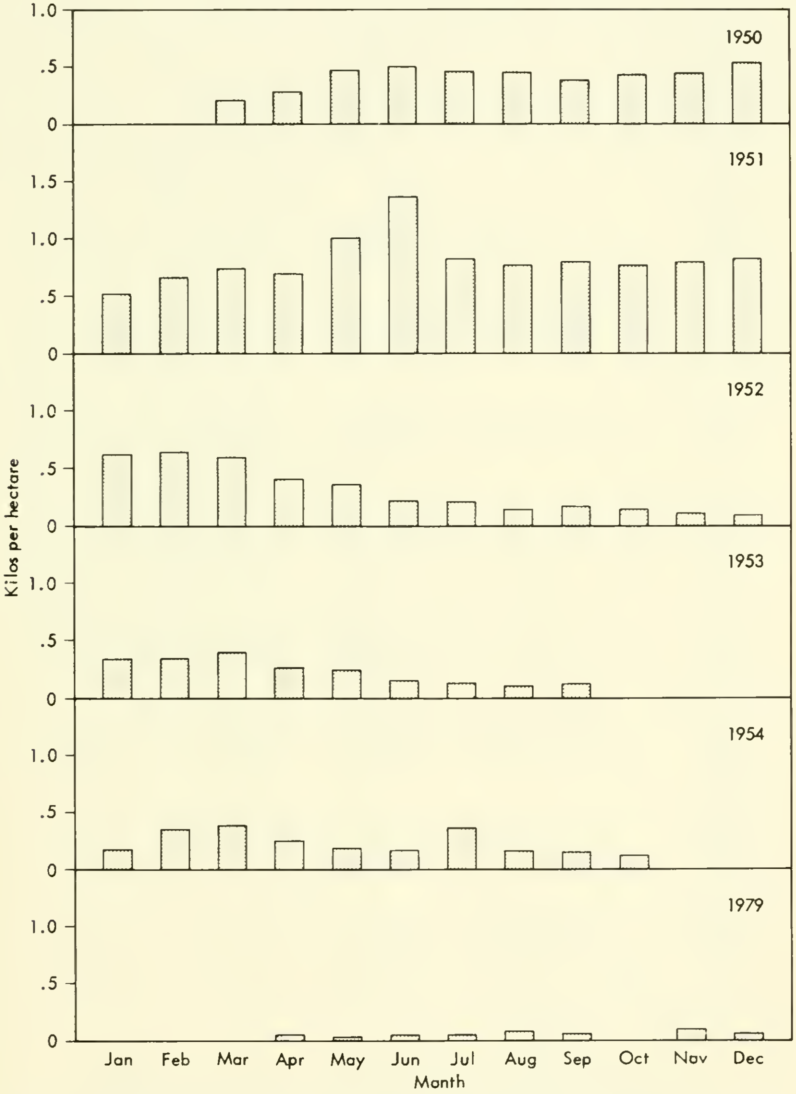

FIGURE 3. Month-to-month changes in combined biomass of small mammal populations of study plot, March 1950 to October 1954, and in 1979.

TABLE 7. Monthly Biomass Estimates (grams/hectare) of Six Rodent Species on House Field during 1950–1953.

	Date											
Species	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
1950												
Prairie Vole	962.5	1840.0	3200.0	3905.0	3820.0	3785.0	3040.0	2900.0	3600.0	3870.0	3885.0	4655.0
Western Harvest Mouse	466.5	230.7	734.2	633.3	473.0	471.0	261.6	437.6	237.6	551.3	565.5	579.0
Pine Vole	250.0	240.0	250.0	31.0	–	20.0	21.0	348.5	156.5	108.5	199.5	680.0
Hispid Cotton Rat	–	–	2.0	3.0	3.5	2.0	0.5	120.0	80.0	40.0	–	–
White-footed Mouse	89.0	360.0	251.5	397.5	165.0	201.0	270.0	393.0	282.5	605.0	447.5	532.5
Deer Mouse	198.5	159.5	265.5	111.0	175.0	93.5	112.0	106.0	120.0	180.0	208.5	92.5
	1966.5	2830.2	4703.2	5080.8	4636.5	4572.5	3705.1	4305.1	4476.6	5354.8	5306.0	6539.0
1951												
Prairie Vole	5580.0	4625.0	7400.0	8275.0	5725.0	4615.0	4225.0	3600.0	3700.0	4905.0	3660.0	4155.0
Western Harvest Mouse	490.0	322.7	255.0	196.0	300.0	190.0	40.0	405.0	625.0	415.0	370.0	215.0
Pine Vole	955.0	907.0	670.5	–	490.0	392.0	549.5	613.5	411.0	487.5	545.0	705.0
Hispid Cotton Rat	–	–	880.0	3960.0	1260.0	1896.0	3080.0	2235.0	2255.0	1540.0	962.5	614.0
White-footed Mouse	430.0	1030.0	565.0	776.0	308.5	570.0	140.5	637.0	880.0	725.0	885.0	761.5
Deer Mouse	44.25	117.5	186.0	149.0	93.5	20.5	–	–	32.5	24.5	48.0	64.0
	7499.25	7002.2	9956.5	13356.0	8177.0	7683.5	8035.0	7490.5	7903.5	8097.0	6470.5	6514.5

Table 7. (Concluded)

	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
1952												
Prairie Vole	3750.0	2260.0	2330.0	1272.0	875.0	807.0	1147.0	845.0	829.0	626.0	3550.0	3640.0
Western Harvest Mouse	400.0	260.0	230.0	260.0	720.0	220.0	240.0	160.0	150.0	250.0	90.0	200.0
Pine Vole	565.0	627.5	567.5	222.5	40.0	–	–	–	80.0	–	–	–
Hispid Cotton Rat	940.0	640.0	320.0	80.0	–	–	–	–	–	–	–	–
White-footed Mouse	425.0	254.5	48.0	180.0	360.0	330.0	264.0	390.0	120.0	–	–	–
Deer Mouse	144.0	78.5	49.0	42.5	28.0	14.0	7.0	–	–	–	–	–
	6224.0	4120.5	3544.5	2057.0	2023.0	1371.0	1658.0	1395.0	1179.0	876.0	3640.0	3840.0
1953												
Prairie Vole	3450.0	2100.0	2210.0	1371.0	1000.0	860.0	1140.0	882.0	880.0	703.0	1681.0	2405.0
Western Harvest Mouse	295.0	180.0	110.0	140.0	350.0	100.0	40.0	–	–	–	–	–
Pine Vole	390.0	432.0	200.0	–	–	20.0	30.0	–	–	–	–	–
Hispid Cotton Rat	–	–	–	–	–	–	–	–	–	–	–	–
White-footed Mouse	–	–	–	–	–	–	–	–	–	–	–	–
Deer Mouse	–	–	–	–	–	–	–	–	–	–	–	–
	4135.0	2712.0	2520.0	1511.0	1350.0	980.0	1210.0	882.0	880.0	703.0	1681.0	2405.0

numbers indicated by capture-recapture indices, and the average weight of the captured animals of each species, with the assumption that those present but not captured, averaged the same. The figures represent the active and mobile part of the population, excluding young in the nest, but these must have made up an appreciable part of the total at most times. The Prairie Vole's biomass was consistently the greatest and usually amounted to several kilos, whereas the harvest mouse was consistently less than one kilo. The cotton rat suddenly came into prominence in the late spring of 1951, and increased while the vole was declining during that summer, and by September had reached 73% of the vole's figure, but then declined, and had disappeared from the plot by July 1952.

As shown in Table 6, the Prairie Vole's numbers increased rapidly in the spring of 1950, declined only slightly in the following autumn, and then increased to a peak population in June 1951. It declined in late summer and autumn of 1951 and underwent further severe decline from June to December 1952, during a period of drought. After making a modest recovery in winter and spring of early 1953, it declined through late 1953 to new lows in 1954.

Figure 4 shows weights of adult Prairie Voles over a three-year period, 1950–52, including a time of unusually high precipitation in the summer of 1951 and the drought of 1952. Maximum and mean weights were much higher during the time of high precipitation and high population levels in 1950 and 1951 than they were in 1952 with drought and low population levels. Maximum and mean weights were usually higher in female voles than in corresponding samples of males, presumably because many of the females were pregnant, but in December 1950, January and March 1951 and August and December 1952, males averaged a little heavier than their female counterparts. In each of these months most or all of the female voles were non-pregnant. For the purpose of this comparison all voles weighing 30 grams or more were considered adults and those of less than 30 grams were excluded as subadults or juveniles.

The diminutive Western Harvest Mouse was usually second in abundance, and in March 1950 and July and December 1952 it outnumbered the Prairie Vole. Compared with other species on the study plot, its population was relatively stable. However, censusing was made difficult by the changing degree of bait acceptance during the annual cycle. In summer these mice seemed to prefer abundant natural foods, including insects, over the grain baits used in the traps, and they were much harder to catch than in the cooler part of the year. Those that were trapped in summer were likely to be the older individuals present, conditioned to the grain bait, and hence the capture-recapture ratio may have been distorted. After July 1953 numbers of these harvest mice on the plot dwindled abruptly.

The Pine Vole was present in relatively small numbers (Table 6) and limited to one edge of the study plot. Its numbers were few in 1950, relatively high throughout 1951 and the spring of 1952, and extremely low in the latter half of 1953 and in 1954. However, by 1955 this vole had

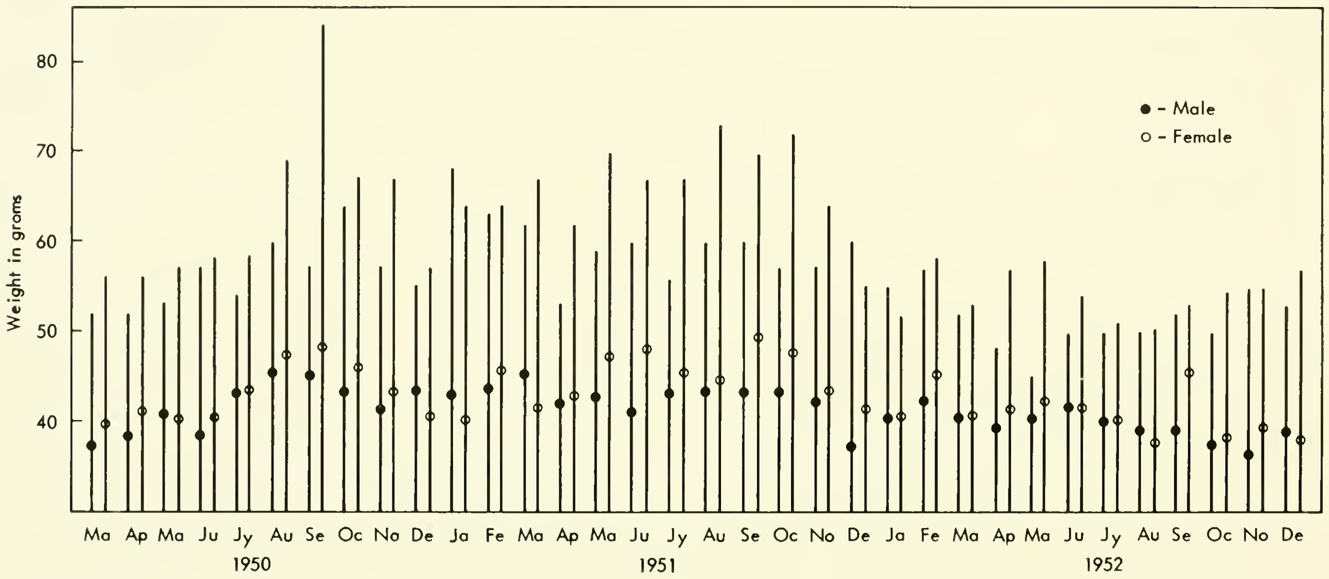

FIGURE 4. Mean and range of weights of adult male and female Prairie Voles over a 3-year period on the study plot; left column of each pair shows males and right column shows females.

partially regained its losses; nine were captured in March, and in April all of these nine and 13 others were captured.

The White-footed Mouse was present in moderate numbers in 1950, increased in 1951 and then underwent gradual decline in 1952, 1953 and 1954. This decline occurred despite the spread of woody vegetation onto the study plot, involving an extension of habitat for this species. Evidently the drought conditions in 1953 and 1954 delayed the spread and increase of this mouse. By 1979 this woodland species comprised most of the population of small mammals on the study plot, but its relative gain was attained by a dwindling of the other species rather than by any marked change in the numbers of White-footed Mice (Table 6).

The Deer Mouse was moderately abundant on the study plot in 1950, and with some irregular fluctuation in each year, underwent year-to-year decrease until only one or two individuals remained late in 1954. Growth of the luxuriant grass-weed crop in the wet year of 1951 and subsequent encroachment of woody vegetation onto the plot constituted stages in habitat deterioration for this mouse. Scanty precipitation and relatively sparse vegetation in 1952–54 presumably delayed its eventual elimination.

Demographic patterns. The species of small mammals studied were all alike in having: 1) short gestation period, approximately three weeks (except for the 27-day period of the Hispid Cotton Rat), 2) rapid development and early maturity (within one to three months of birth), 3) long breeding season, individuals contributing offspring to the population within the season of their own birth, 4) rapid population turnover, only a small percentage of animals surviving for a full year.

Figures 5 and 6 bring out some important differences. Most of the Hispid Cotton Rats recorded were juveniles at first capture as these rats are precocial, become independent when only a few days old, and hence are at risk to live-traps from an early age. The samples of Deer Mouse, White-footed Mouse, and Western Harvest Mouse, in that order, each contained substantial numbers of animals that were above average adult size at first capture. Presumably many of these were immigrants to the study plot from nearby areas in these moderately vagile species. On the other hand, the Prairie Vole is so sedentary that many individuals born within the area of the trap grid are believed to have grown to maturity in the same home range between adjacent traps without ever having contacted a trap.

Breeding data are shown in Table 4. Figures in parentheses show number of adult females in the sample. Each species differs somewhat from the others in the extent and timing of its annual breeding season. Also, each species is subject to major changes from year to year in the intensity and duration of the breeding season, occasioned by direct effects of the weather, the food supply, and perhaps sociological factors. All species show somewhat parallel trends in having reproduction stopped or at low ebb in the coldest part of the year, but rising rapidly to a maximum level in late winter or early spring, declining somewhat in the hottest part of the year. All have potentiality for multiple litters, and females born

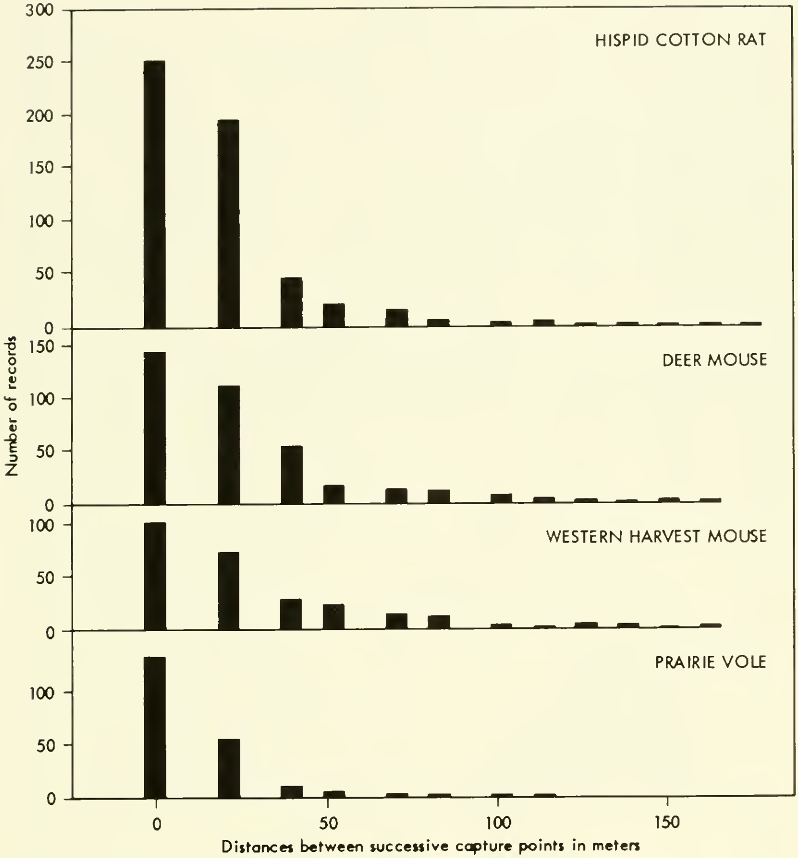

FIGURE 5. Histogram comparing vagility (as indicated by distance between successive capture points) in four species of small mammals on study plot, 1950–52.

early in the year may mature and produce their own litters late in the season.

When small mammal populations were high on the study area, the Prairie Vole was usually most abundant. Its numbers were subject to rapid change. Increase and spread began in 1949, when the former pasture, protected from grazing, produced a heavy crop of herbaceous vegetation providing food and cover. A 0.2 ha fenced plot of tall grass adjacent to the eastern end of the study plot was known to have a few of these voles in 1948, and presumably those on the plot originated from that nucleus.

Reproduction in this vole occurs throughout the year but is at its annual peak in spring and is lowest in midwinter. In their reproductive condition the voles are highly responsive to both the weather and the quality of available food. In mild spring weather, with an abundance of succulent food of high protein content, males have enlarged scrotal testes and females are often simultaneously lactating and pregnant. In periods of

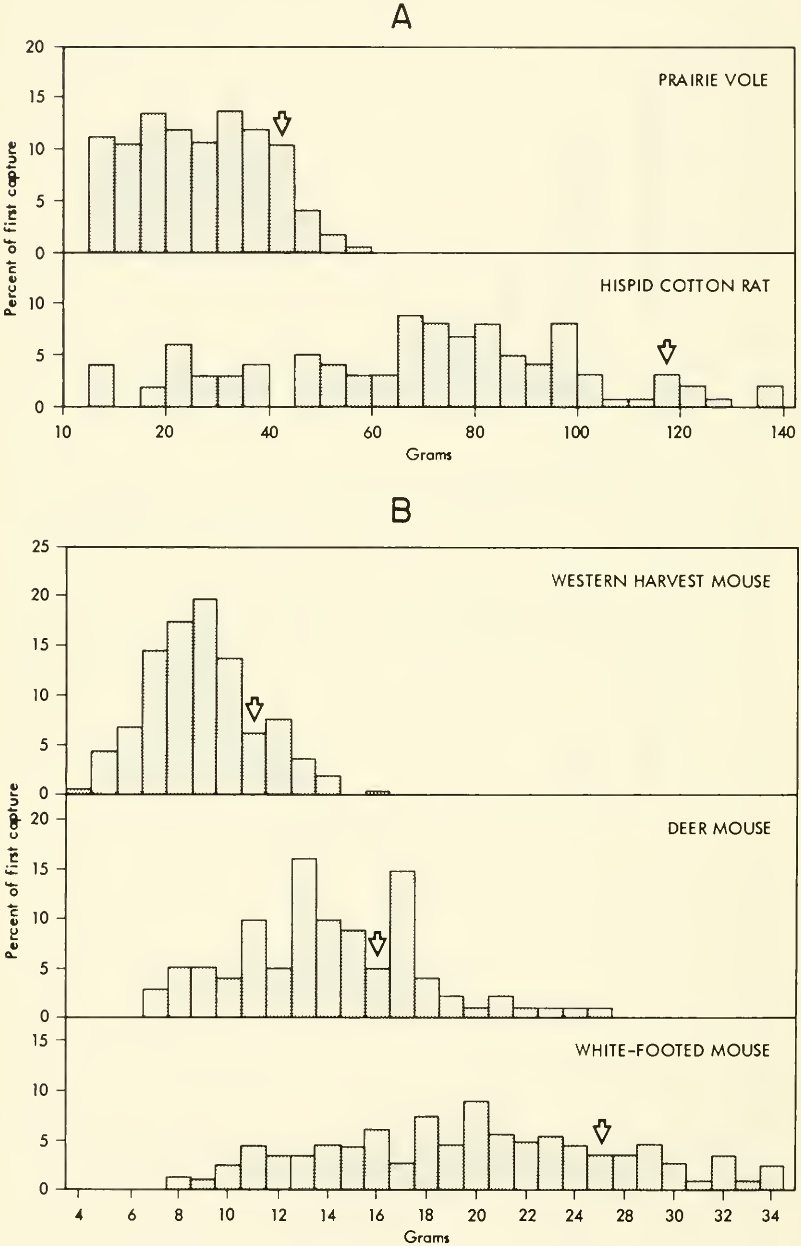

FIGURE 6. Histogram comparing weights at first capture for 5 species of small mammals on study plot, 1950–52. Arrows indicate average adult weight for each species. The majority of individuals present were caught and marked before reaching adult size. a. Prairie Vole and Hispid Cotton Rat. b. Western Harvest Mouse, Deer Mouse, and White-footed Mouse.

summer drought, such as in August 1952, when vegetation becomes coarse and fibrous with low protein content, weights of voles decline and reproduction stops. Cannibalism on newborn young by adult males is severe during drought and may lower population levels.

The ratio of reproductive females changed from year to year and month to month. High reproductive ratios (exceeding 70%) occurred in February 1954, March 1952, and April 1950 and 1953. Low ratios (less than 20%) occurred in January 1952, July 1952 and 1953, August 1952, and December 1950 and 1954. Order of months from the highest to lowest in level of reproductive activity was: April, May, March, September, October, February, June, August, July, January, November, December. Months within the seasons, February-March-April-May and September-October, consistently had ratios near or exceeding 50%, but early winter and late summer ratios were sometimes much lower.

In summary, the Prairie Vole breeds throughout the year but with fluctuating levels, their maxima often three to six times their minima, with highest and least variable ratios in spring and early autumn. Living a partly subterranean existence, and having the habit of food storing highly developed (second only to the Pine Vole), the Prairie Vole is somewhat buffered against extremes of temperature and moisture, and may be less responsive to weather than other kinds of rodents studied.

Conclusions regarding breeding in the Pine Vole are hindered by small samples in 1951 and early 1952 and lack of samples for most other times. As in the Prairie Vole, there is some breeding through most of the year, but only one of 14 in November 1951 was in oestrus and none of six in December. Highest ratios of reproductive individuals were 80% (April 1952), 71.5% (March 1953), and 66.6% (September 1951). As the most fossorial of the 13 species studied, and the one having the storage habit most highly developed, the Pine Vole is to some extent buffered against the rigors of the terrestrial environment and may be less sensitive to seasonal changes than most other species.

On our study plot the Hispid Cotton Rat is near its northern range limits (Cockrum, 1948; Genoways and Schlitter, 1967). Depending on the severity of the winter, a high percentage of the autumn population may be eliminated. The species occurs in habitats having tall weedy plants and feeds mainly on succulent herbage of the same types taken by Prairie Voles (Fleharty and Olson, 1969; Menhusen, 1969; Terman, 1978). However, animal food is also taken. On many occasions the predatory tendencies of cotton rats were demonstrated when one caught in a trap along with a vole or harvest mouse had killed and partly eaten the smaller animal. The cotton rat's precocial development may confer some competitive advantage over associated rodent species.

Cotton rats were caught on the study plot in numbers adequate for reproductive samples only from June 1951 through March 1952. A striking aspect of the reproductive cycle is that breeding stops in the colder part of the year. There were no reproductive individuals in the samples through December, January, February, and March, and only 10 of the 127 females in November were reproductively active. Trapping in other years on nearby areas has confirmed that there is but little breeding activity in November, and, in fact, has indicated that the incidence of breeding decreases drastically in the latter half of October in some years. April–May and August–September were the peak months of reproductive activity, with 70% to 100% of females in oestrus.

The Western Harvest Mouse, like the Prairie Vole, is believed to have reached the study plot from a small fenced area adjoining it on the east end. When habitat conditions became favorable after removal of livestock in 1949, the species spread over the plot rapidly and increased. Our samples included one or more reproductive individuals from each month of the year. However, the samples, insofar as they are adequate, indicate low levels of reproduction in December, January, and February. Each of these months lacked reproductive individuals in at least one of the years sampled. April had the highest incidence of breeding and August was second. In the spring and summer of 1950, reproduction was maintained at a higher level than in subsequent years.

Throughout the study the White-footed Mouse was usually as abundant in adjacent woodlands as it was on the study plot. In 1950 nearly all caught on the plot were along its margins within a meter or two of woodland. In 1951, after brush had begun to invade the plot, these mice were caught more frequently and some were farther out in the field. They were present in nearly all parts of the field by 1979, but the population, both there and in the adjacent woodland, was low. Samples indicate a breeding season beginning in February and continuing at a high level into September. Females were rarely in oestrus in October, November or December and none (of 15) was in oestrus in January. March–April, June and August–September were peak months of reproduction with the incidence of females in oestrus near or exceeding 50% in each.

The Deer Mouse was probably present in low densities while the plot was still subject to grazing. It was caught in increasing numbers in 1950 and 1951, decreased slightly in 1952, and increased again in 1953. Plant succession resulted in habitat deterioration for the species as ground cover became more dense and intervening bare patches disappeared. By 1954 few Deer Mice remained on the plot and in subsequent years none was recorded. The species was noteworthy for year-round breeding, with a substantial proportion of females (17.6%–61.5%) in oestrus in each month except December (5.3%). August (61.5%), September (37.6%), March 31.0%), May (27.3%), June, July, and October (each 25.0%) were the months of greatest breeding activity.

Habitat selection. For each species of small mammal, records were unevenly distributed within the study plot, as certain trap sites yielded none whereas other favored sites yielded disproportionately large numbers, more than 20% of the total for a species in some instances. The several species tended to be complementary in their distribution on the plot, as no two had their records concentrated at the same spots.

Figures 7 and 8 show the distribution of records for the Prairie Vole and Western Harvest Mouse, respectively, on the area and similar maps were made for the other species. Each figure at a trap site represents the

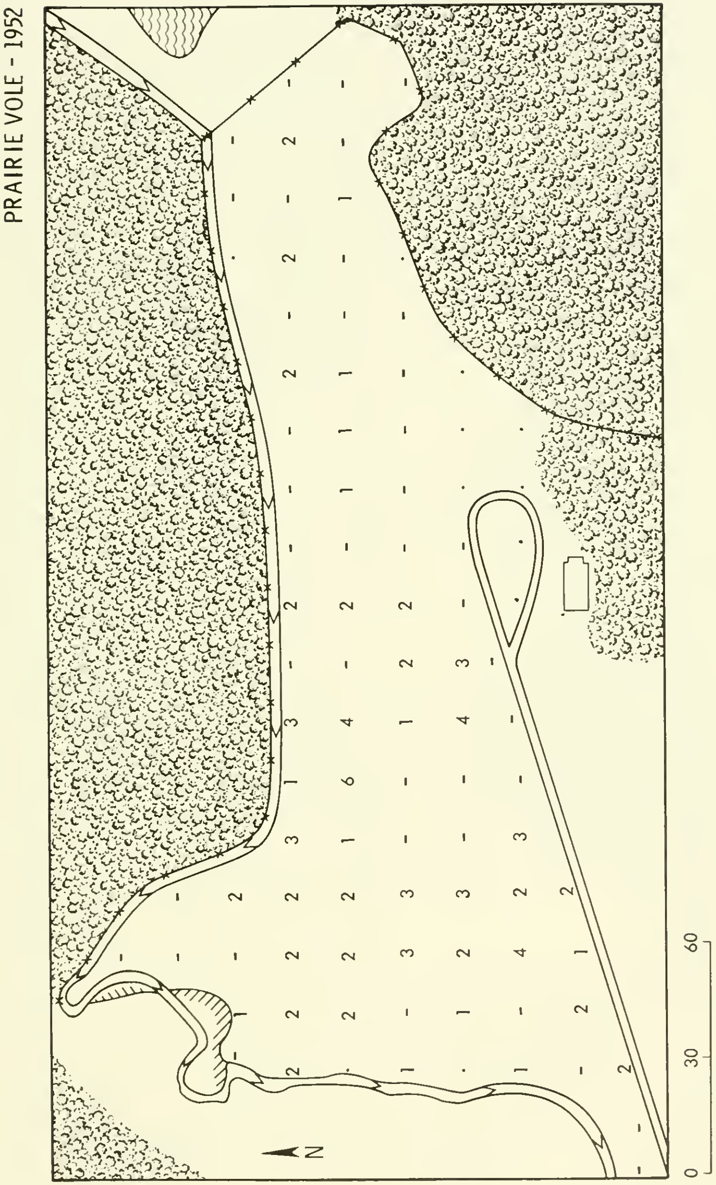

FIGURE 7. Map of study plot showing distribution (by percentages of the 1639 captures made in 1952) of Prairie Voles on trap grid. Dots show trap locations where no captures were made, minus signs indicate captures that amounted to less than half of one per cent of the total.

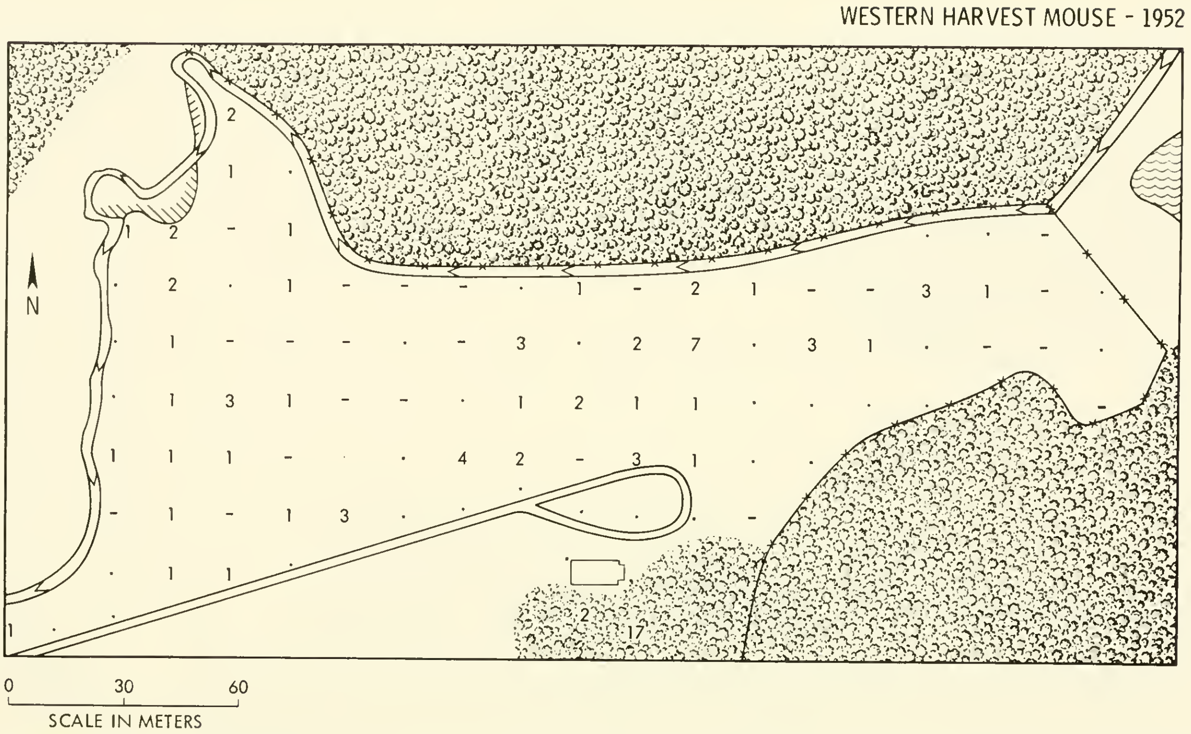

FIGURE 8. Map of study plot showing distribution (by percentages of the 401 captures made in 1952) of Western Harvest Mouse on trap grid (symbols as in Fig. 7).

percentage of the species-sample recorded from that specific location with figures rounded to the nearest whole number. A minus sign indicates that the species was taken at the site shown, but in numbers amounting to less than half of one per cent of the species-sample. The Prairie Vole occurred on all parts of the plot, but its density was markedly higher on the western half than on the partly shaded eastern half. The maximum catch of 6% was at an open grassy site dominated by Smooth Brome. The Western Harvest Mouse also occurred on all parts of the plot but the trap sites that were most productive were partly shaded by large elms with Kentucky Bluegrass and Muhly Dropseed prominent. The Hispid Cotton Rat also was found on all parts of the plot, but one trap site yielded 23% of the total sample, another 12%, reflecting the tendency to bait addiction and trap habit more strongly developed in this species than any other (Fitch, 1958). The Deer Mouse was confined to the parts of the plot having the shortest and sparsest vegetation; all records were in the western half, and 98% were in the area that had been stripped of sod many years before, and had an impoverished plant community, mainly of Common Lespedeza and Threeawn Grass, with patches of bare soil. One-third of the entire sample was obtained from three adjacent trap sites. The White-footed Mouse was captured mainly along the southeastern edge of the plot, near or beneath large American Elms, and often near thickets of Blackberry and/or Coralberry. The Pine Vole was caught chiefly in the narrow eastern one-third of the plot, usually in the shade of American Elms with records concentrated at a few sites which probably were interconnected as part of one burrow and runway system, or may have belonged to two such systems.

The several rodent species were possibly influenced in their local distribution by each other as well as by the vegetation and the physical environment. Table 8 provides figures showing amount of spatial overlap between the samples of the six common species. "Percentage of overlap" is based on the percentages of samples shown on the maps, Figures 7 and 8 (for the Prairie Vole and Western Harvest Mouse), and similar maps (not included here) for the other species. For each species-pair the pair of figures available for each shared site of occurrence was averaged and all these averages were totalled to obtain the figure for "percentage of overlap."

Overlap was found to be greatest (52.5%) between the Prairie Vole and Deer Mouse, and was also relatively high in other pairs when both animals were characteristic of the same general type of habitat, whether grassland or forest edge, but was low (down to zero overlap) in species characteristic of different habitat types. The lowest figure for two animals of the same general habitat type was 14.5% for the Deer Mouse and the Western Harvest Mouse; both are grassland animals but the former prefers shortgrass habitat, the latter, tallgrass, locally.

Spatial relationships. Table 3 and Figure 5 compare movements in four species and it is shown that the Prairie Vole is much less vagile than the Hispid Cotton Rat, Western Harvest Mouse, or Deer Mouse. Ordinarily an individual vole limits its movements to its system of under-

TABLE 8. Habitat Overlap of Six Small Mammal Species on Study Plot.

	Prairie Vole	Hispid Cotton Rat	Western Harvest Mouse	Pine Vole	Deer Mouse	White-footed Mouse
Trap stations	79	52	61	25	33	29
Captures	1639	621	401	905	148	190
Prairie Vole	XXXX	32.5	40.5	13.5	52.5	8.5
Hispid Cotton Rat	47	XXXX	35.5	47.0	15.5	19.0
Western Harvest Mouse	57	39	XXXX	25.0	14.5	3.5
Pine Vole	15	12	13	XXXX	0	44.0
Deer Mouse	24	15	27	1	XXXX	0
White-footed Mouse	9	7	7	9	0	XXXX

PERCENTAGE OF OVERLAP

NUMBER OF TRAP STATIONS SHARED

ground and surface runways; 63% of recaptures were at the same spot as the preceding capture and an additional 26.8% were at one of the adjacent grid positions (15.3 m if in the next trap of the same row, 21.7 m if in the diagonal position on a neighboring row).

For the Hispid Cotton Rat 47.7% of recaptures were at the same spot as the preceding capture (no movement); the corresponding figures were markedly lower in the Deer Mouse (38.9%) and the Western Harvest Mouse (36.9%). The longest movements recorded were made by the Hispid Cotton Rat, the second longest were those of the Deer Mouse, and the Western Harvest Mouse was third.

Table 3 compares vagility in the sexes in four species. In the Prairie Vole females are slightly more vagile than males, that is, they have larger home ranges. On the contrary, in the Hispid Cotton Rat, Western Harvest Mouse, and Deer Mouse, males are more vagile. The greatest sexual difference was found in the Deer Mouse, in which male movements averaged nearly twice female movements. These figures suggest that male ranges are nearly four times as large as female ranges.

Many of the captures of Pine Voles that we recorded were in traps specially placed in the vole runways rather than the regular positions in the grid. The White-footed Mice captured were often at the edges of the plot, and presumably each individual had a home range that was mostly in woodland habitat beyond the borders of the plot. Consequently, the records of movements that we obtained for these two species are not strictly comparable with the data obtained for the remaining four species, as shown in Table 3 and Figure 5.

DISCUSSION AND CONCLUSIONS

Data gathered in the course of our study focused on determining the kinds and numbers of small mammals present at different times and correlating these with plant succession as the area progressed from a weedy overgrazed pasture to a tall-grass meadow, then to a grass-and-shrub mosaic and finally to woodland. Comparative data on reproduction, movements, survivorship and microhabitat were gathered for all of the species, and were used in attempting to understand how the observed changes took place. Effects of the normal seasonal cycle on small mammal populations were observed, and distinguished from longtime successional trends. During the course of our field work, extremes of weather with cold, heat, drought, and unusually heavy precipitation occurred and affected populations of small mammals, sometimes by causing outright mortality and sometimes by either accelerating the longtime successional trends or delaying or temporarily reversing them. Intraspecific interactions were found to change according to season, population density and other factors. Interspecific interactions, occurring between members of each species-pair, were trivial in some instances but in other instances may have involved competition for food, or even predation.

At the start, in 1948, the small mammal community was depauperate in both species and individuals. Thirty-two years later it was only a little better represented, but in the interim it had undergone a dynamic and drastic change. The trend was one of rapid increase for approximately the first three years, to a peak in early summer of 1951, then decrease, rapidly at first and later more slowly, with progressive loss of species.

The peak population came at a relatively early stage of succession, in the third growing season after release from grazing pressure by livestock, when the vegetation was at its maximum diversity and the herbaceous component was near its maximum biomass. Of the six common small mammal species, one (Deer Mouse) attained its peak in numbers early in the second growing season (May, 1950) and four others in the second growing season. The sixth (Western Harvest Mouse) was near its peak early and late in the third growing season, but attained its maximum in the fourth season. In general, replacement of grass and forbs by trees and shrubs involved habitat deterioration for small mammal populations, since only four of the 13 kinds trapped on the area occur regularly in forest.

Three sorts of changes, two of them predictable, affected this small mammal community. First, there were the regular sequences of the annual cycle, from hot to cold, from wet to dry, and vice versa. Superimposed on these regular and rapid changes were the much more gradual long-term changes brought about by plant succession. Finally, there were unpredictable vagaries of the weather, with extremes of moisture and temperature of varying duration and severity. Small mammals were found to be highly responsive to each of these types of changes, and all the population changes that we noted could logically be attributed to their interactions.

On many occasions we observed that rain, drought, heat or cold could, within a few days, effect noticeable change in the general condition of the animals and the incidence of reproduction. In the Prairie Vole, for instance, a sequence of several unseasonably mild days in January and February could trigger onset of oestrus in many females at the time of year when most were sexually inactive. Conversely, a sequence of hot and dry weather in late summer could cause a general cessation of oestrus in these voles.

The annual cycle of seasons which was the basis for important changes in the small mammals' reproduction, food habits, and general behavior, might be expected to lead to an annual cycle in numbers. Reproduction beginning in early spring and adding successive increments of young until late autumn could culminate in an annual fall peak. Actually no such tendency was revealed in any species. It seemed that various mortality factors, especially density-dependent predation, prevented such a pattern. Peak numbers might occur in almost any month, and did not recur at the same time from year to year.

Predation was probably a major factor in population trends, but its total impact and the relative importance of different species of predators was difficult to judge. When small mammals were near their peak numbers in 1950 and 1951, their predators, too, were remarkably numerous and conspicuous in the area. Domestic cats from nearby farms or gone feral (mostly adult males) were seen frequently. Even though cats were shot on sight, those eliminated were quickly replaced in a seemingly endless succession. Coyotes and both Red and Gray Foxes caught many small mammals, judging from their sign. The Barred Owl was the most important raptor, with always one or two pairs centering on the area. The Copperhead, Yellow-bellied Racer, Black Rat Snake, Red-sided Garter Snake and Prairie King Snake, in that order of importance, were all major predators on small mammals. The Red-tailed Hawk, Spotted Skunk and Timber Rattlesnake, though present on the area from time to time, are thought to have played relatively minor roles compared with those kinds previously listed.

These predators differed in their responses to population changes in the small mammals. The cats and canids especially were highly mobile, and converged on the area with concentrated effect when prey populations were high. The Red-sided Garter Snake is usually thought of as a predator on earthworms and amphibians, but large adults (usually females) were found to take small mammals, which constitute an important part of the species' prey biomass locally. The garter snake's effectiveness as a predator on small mammals is dependent on its abundance, often 2–7 adults per ha (Fitch, 1965) and relatively short generation time (maturity attained in second year) permitting it to respond more rapidly than most mammal-eating snakes to changes in numbers of its prey. Five species of rodent-eating snakes were calculated to have a combined population density of nearly 17 per ha in the general area, and taking into account their numbers, and frequency and amount of feeding, their combined annual predation was calculated to amount to a biomass of more than three kilograms of the six common small mammals (Fitch, 1982). Obviously, predation by snakes is a major factor influencing population trends in small mammals during the warmer half of the year.

Each year of the study was sufficiently different to elicit a different response from the small mammal population. Each year ushered in a more advanced stage of succession, with mammal populations somewhat altered from any equilibrium they might have attained previously. The changes that we have observed on the area are progressive and not readily reversible. Each assemblage of species and combination of population levels that we have observed seems to be unique to its point in time.

Various degrees of overlapping in habitat and food habits occurred between the various species of small mammals, but some of the most important interactions may have involved predation by cotton rats on the smaller species. Stoddard (1931) noted that the rats' diet, mainly of herbage, is regularly supplemented by animal food, and Martin (1956), working on a study plot adjacent to our own, obtained circumstantial evidence of cotton rat predation on nestling voles as a major factor in the decline of the vole population in 1951.

Cotton rats appeared in April 1950 and increased rapidly through the summer and early fall. As the cotton rat population came into prominence, numbers declined in other species, notably the Prairie Vole. By September 1951, the cotton rat biomass had increased to 75% of the vole's, but thereafter, cotton rat numbers dwindled, with the greatest decrease in December and few remaining by January 1952.

The competitive relationship between the Hispid Cotton Rat and the Prairie Vole has been the subject of extensive observation, experimentation and speculation by various authors (Menhusen, 1969; Fryendall, 1969; Fleharty and Olson, 1969; Baker, 1971; Terman, 1974 and 1978; Glass and Slade, 1980a and 1980b; and Prochaska and Slade, 1981). From the findings of these investigators it is known that the two species are ecologically similar, overlap widely in food habits, and compete, but that voles tend to avoid cotton rats while the latter tend to behave aggressively toward voles, with pursuit, attack, and occasional maiming or outright killing.

As already indicated, the populations of each species changed rapidly throughout our study. There were long-term trends in each, but with short-term fluctuations that sometimes involved temporary reversals of the long-time trends. However, no periodicity was discernible. No population peaks comparable to those of 1951 were attained again in the next 30 years in any of the six common species.

The existence of population cycles in small mammals is well established (Elton, 1927; Pitelka et al., 1955; Chitty, 1960; Krebs et al., 1973; Krebs and Myers, 1974), and is especially evident in Arctic and subarctic animals. Various species of voles (*Microtus* spp.) are known to be subject to drastic fluctuations in numbers which have been interpreted as cycles in many instances (Krebs et al., 1973; Krebs and Myers, 1974; Rosenzweig and Abramsky, 1980). Even the Prairie Vole at the latitudes of Indiana and Kansas has been considered cyclic (Krebs et al., 1973; Gaines and Rose, 1976; Abramsky and Tracy, 1979). Gaines and Rose (1976) monitored populations of Prairie Voles on four separate study plots (all within 2 km of the plot in the present study) over a four-year period. They noted parallel changes on all plots, with two population peaks, and interpreted their data as supporting a two-year cycle. However, our own observations suggest that in the general area of our study, in Douglas and Jefferson counties, Kansas, each small, isolated vole population develops independently and asynchronously from others, depending on the stage of succession and land use in the local habitat as well as the weather sequence.

In California, at approximately the same latitude as that of our study, Garsd and Howard (1981) made a 19-year study of a vole population and noted constant fluctuation but no regular cycles. They concluded that fluctuations were random and that the voles studied were regulated by a highly complex system of variables on both the intrinsic and ecosystem levels. A similar conclusion seems appropriate for the changes actually observed in the Prairie Vole population during the course of our study.

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APPENDIX I

List of plants prominent in succession of study plot

American Elm *Ulmus americana* L.
American Germander *Teucrium canadense* L.
Aster *Aster ericoides* L.
Barnyard Grass *Echinochloa crusgalli* (L.) Beauv.
Big Bluestem *Andropogon gerardii* Vitman
Blackberry *Rubus flagellaris* Willd.
Black Walnut *Juglans nigra* L.
Broomsedge *Andropogon virginicus* L.
Buffalo-bur *Solanum rostratum* Dun.
Carolina Nightshade *Solanum carolinense* L.
Cheese Mallow *Sida spinosa* L.
Common Lespedeza *Lespedeza bicolor* Turcz.
Common Ragweed *Ambrosia artemisiifolia* L.
Common Sunflower *Helianthus annuus* L.
Coralberry *Symphoricarpos orbiculatus* Moench
Crabgrass *Digitaria sanguinalis* (L.) Scop.
Curly Dock *Rumex crispus* L.
Elderberry *Sambucus canadensis* L.
Flowering Spurge *Euphorbia corollata* L.
Fox Grape *Vitis vulpina* L.
Giant Ragweed *Ambrosia trifida* L.
Goatweed *Tragia betonicifolia* Nutt.
Greenbrier *Smilax hispida* Muhl.
Green Foxtail *Setaria viridis* (L.) Beauv.
Ground Cherry *Physalis heterophylla* Nees.
Hackberry *Celtis occidentalis* L.
Honey Locust *Gleditsia triacanthos* L.
Hoary Vervain *Verbena stricta* Vent.
Ironweed *Vernonia baldwini* Torr. var. *interior* (Small) Schub.
Japanese Chess *Bromus japonicus* Thunb.
Kansas Milkweed *Asclepias syriaca* L.
Kentucky Bluegrass *Poa pratensis* L.
Kentucky Coffee Tree *Gymnocladus dioica* (L.) K. Koch
Little Bluestem *Andropogon scoparius* Michx.
Missouri Goldenrod *Solidago missouriensis* Nutt.
Muhly Dropseed *Muhlenbergia schreberi* Gmel.
Mulberry *Morus rubra* L.
Osage Orange *Maclura pomifera* (Raf.) Schneid.
Philadelphia Fleabane *Erigeron philadelphicus* L.
Pokeweed *Phytolacca americana* L.
Purpletop *Tridens flavus* (L.) Hitchc.
Red Cedar *Juniperus virginiana* L.
Rough-leafed Dogwood *Cornus drummondii* C. A. Mey.
Sedge *Carex* sp.
Smooth Brome *Bromus inermis* Leyss.
Smooth Sumac *Rhus glabra* L.
Snow-on-the-mountain *Euphorbia marginata* Pursh
Stinkgrass *Eragrostis cilianensis* (All.) E. Mosher
Sumpweed *Iva annua* L.
Tall thistle *Cirsium altissimum* (L.) Spreng.
Threeawn Grass *Aristida oligantha* Michx.
Virginia Creeper *Parthenocissus quinquefolia* (L.) Planch.
Wild Crab Apple *Pyrus ioensis* (Wood) Bailey
Wild Lettuce *Lactuca serriola* L.
Wild Plum *Prunus americana* Marsh.
Witchgrass *Panicum capillare* L.
Woolly Croton *Croton monanthogynus* Michx.

APPENDIX II

List of mammals mentioned in text

Brown Lemming *Lemmus sibiricus* Kerr

California Vole *Microtus californicus* (Peale)

Coyote *Canis latrans* Say

Deer Mouse *Peromyscus maniculatus* (Wagner)

Eastern Cottontail *Sylvilagus floridanus* (J. A. Allen)

Eastern Mole *Scalopus aquaticus* (L.)

Eastern Wood Rat *Neotoma floridana* (Ord)

Fox Squirrel *Sciurus niger* L.

Gray Fox *Urocyon cinereoargenteus* (Schreber)

Gray Squirrel *Sciurus carolinensis* Gmelin

Great Plains Harvest Mouse *Reithrodontomys montanus* (Baird)

Hispid Cotton Rat *Sigmodon hispidus* Say and Ord

House Mouse *Mus musculus* L.

Least Shrew *Cryptotis parva* (Say)

Long-tailed Weasel *Mustela frenata* Lichtenstein

Meadow Jumping Mouse *Zapus hudsonius* (Zimmermann)

Meadow Vole *Microtus pennsylvanicus* (Ord)

Opossum *Didelphis marsupialis* L.

Pine Vole *Microtus pinetorum* (Le Conte)

Plains Pocket Gopher *Geomys bursarius* (Shaw)

Prairie Vole *Microtus ochrogaster* (Wagner)

Raccoon *Procyon lotor* (L.)

Red Fox *Vulpes vulpes* (L.)

Short-tailed Shrew *Blarina hylophaga* Elliot

Southern Lemming Mouse *Synaptomys cooperi* Baird

Spotted Skunk *Spilogale putorius* (L.)

Striped Skunk *Mephitis mephitis* (Schreber)

Varying Hare *Lepus americanus* Erxleben

Western Harvest Mouse *Reithrodontomys megalotis* (Baird)

White-footed Mouse *Peromyscus leucopus* (Rafinesque)

White-tailed Deer *Odocoileus virginianus* (Zimmermann)

Woodchuck *Marmota monax* (L.)

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